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Original investigation

Specificity of non-metric parameters of American mink (*Mustela vison*) populations in relation to habitat differences in Belarus

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Abstract

A total of 418 skulls of the American mink Mustela vison was examined in a non-metric study to reveal the specificity in 15 remote population fragments and for 4 geographical populations inhabiting the large river basins in Belarus. Also, 14 samples from the present population fragments were compared with the sample closely related to the founders of the naturalised populations of this species. The phenetic (non-metric) distances between the samples were estimated using 22 nonmetric traits. High levels of phenetic divergence in the naturalised American mink populations in Belarus were revealed. The founders exhibited significant phenetic differences compared with each of the 14 remote population fragments. Substantial phenetic differences were displayed in half of the pairwise comparisons between remote population fragments. Moreover, among population fragments from a single river basin, there was a significant negative correlation between phenetic similarity and spatial distance. There was no such correlation among population fragments from different river basins. Phenetic distances between all of the 4 geographical populations inhabiting the large river basins were statistically significant. This non-metric differentiation in the naturalised species is discussed with respect to the very diverse and different habitat conditions in which the populations exist. The phenetic plasticity (which marks genetic plasticity) of American mink revealed by our study is an adaptation which determines the high demographic success of this naturalised species demonstrated in many regions of Europe and Asia.

Key words: Mustela vison, population variability, non-metrical parameters, Belarus

Introduction

Studies of intra- and interpopulation variation in genetic and morphologic parameters of naturalised mammalian species are important in contemporary population biology (HARTL et al. 1993 a) and conservation biology (e.g. SCRIBNER 1993). There is now a considerable literature on intraspecific

differentiation in a wide spectrum of mammals (e.g. Rees 1969; SMITH 1981; YABLO-KOV et al. 1983; McLellan and Finnegan 1990; Kozakiewicz and Kanopka 1991; Hartl et al. 1993 b; Ruiz-Garcia 1998). Phenetic variation in mammals, mostly expressed as a non-metric variation of their

skulls, is usually used as a simple and cheap way to study morphologic and genetic differentiation and diversity in mammalian populations (see SJØVOLD 1977, for review). Doubts concerning concordance between phenetic and genetic variation have been raised (e. g. HARTL et al. 1993 b), and many authors note the considerable contribution made by both environmental factors and genetics in the prediction of phenetic differentiation (e. g. Petras 1967; Markowski and Markowska 1988; Soule and Zegers 1996).

The study of intraspecific genetics of introduced species, such as the American mink, Mustela vison, is particularly interesting from both practical and theoretical aspects. Primarily domesticated as a valuable furbearing animal, the American mink started to naturalise in Eurasia during the 1950s (PavLov et al. 1974). In the newly colonised areas, this species exhibited a very high ecological adaptability (GERELL 1967 a, b; Danilov and Tumanov 1976; Ternovsky 1977; CHANIN and LINN 1980; DUNSTONE and Birks 1987: Dunstone 1993: Sidoro-VICH 1993, 1997; TERNOVSKY and TERNOVS-KAJA 1994). Furthermore, relatively shortterm morphological responses by American mink to PCB's (Borisov et al. 1997) and to domestication (KRUSKA 1996; KRUS-KA and SCHREIBER 1999) have been revealed.

In Belarus, the very different habitat conditions in different parts of the country lead us to expect complicated genetic responses and morphological divergence in naturalised American mink populations. The aim of this study was to investigate the non-metric diversity of this species in Belarus, and the non-metric divergence of local populations inhabiting river catchments with different ecological conditions. Also, by analysing the skulls from contemporary local populations, we had rare opportunity to compare them with the sample of skulls collected at the time of the beginning of the naturalisation of American mink in Belarus. Thus, we evaluated both spatial and temporal scales of the non-metric skull differentiation in American mink in Belarus.

Material and methods

Most of the sampling areas were located in central and northern Belarus (Fig. 1). Only one study area was in the south-eastern part of the country. We obtained samples from all the four main river basins of Belarus: the Western Dvina, Dnepr, Pripjat, and Neman. Taking into account species-specific features of habitat selection by the American mink, each of these basins consisted of different habitat conditions.

The Western Dvina river catchment is mainly characterised by fast flowing streams of various sizes. Usually, rivers have no or very narrow floodplains. Glacial lakes and brooks were more abundant in this catchment than in the other three. Both the Neman and Dnepr river basins basically have rivers with moderate flow rates and medium-sized swampy floodplains. The Pripjat river basin is located in the lowlands and has only slowly flowing rivers with highly swampy large valleys. There are considerably fewer small rivers and brooks in this river basin than in the other three.

We also sampled the American mink population in the upper reaches of the Lovat, an area which combined all the features of the four main river basins, and in which American mink lived in conditions of a great diversity of habitats.

In 1987–1995, a total of 393 skulls of American mink from 14 localities was sampled (Tab. 1). Also, we had one sample (25 specimens) from a captive population of this species founded by the American mink released in Belarus for the purpose of naturalisation in 1953–1958. This sample originally derived from one of the biggest American mink farms in Belarus (Molodechno district, Minsk region), and was collected about 1960.

Formation of populations of naturalised American mink in Belarus was influenced by introduction in 1953–1958 and consequent northward and southward expansion from the central part of the country. Escaped ranch animals had a certain influence mostly in the central part of Belarus, where the majority of farms is located (SIDOROVICH 1995). Thus, the Lovat, W. Dvina, and Pripjat geographical populations can be considered as the result of expansion.

We used two methods of analysis. First, we carried out a pairwise comparison of the above-mentioned local populations distributed in the sampled areas (Tab. 1), which was used to reveal a non-metric difference depending on the spatial distance. Second, we investigated skull non-metrical variability of the American mink populations inhabiting the main river catchments to reveal

non-metrical specificity of population in different landscapes. In order to compare American mink inhabiting different habitat conditions, we combined samples from the central regions of Belarus (the Neman and Dnepr), because both catchments are characterised by very similar habitat conditions. Phenetic relationship among local population fragments of American mink was studied in two ways: 1) among samples belonging to the same basin of a large river, and 2) among samples derived from the different basins of large rivers (W. Dvina, Dnepr, Neman, Pripjat).

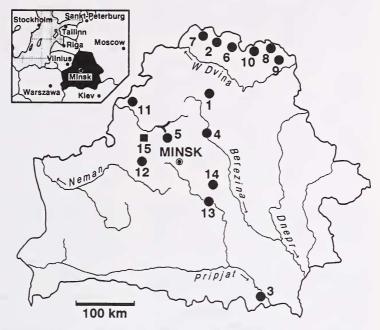


Fig. 1. Study area. Dots show location of samples from the present population fragments; square indicates location of the founder sample. Numbers of samples as in table 1.

Table 1. Information on samples

| Sample | n | Sampling period | Rivers in the sampling area | Main river basin |
|--------|-----|-----------------|---|------------------|
| 1 | 10 | 1991-1992 | Ushacha | West. Dvina |
| 2 | 69 | 1987-1993 | Nishcha, Akhonka, Lemenka | West. Dvina |
| 3 | 15 | 1990-1993 | Zhelon, Slovechna, Pripjat | Pripjat |
| 4 | 26 | 1990-1994 | Brodnia, Gaina, Eastern Berezina | Dnepr |
| 5 | 22 | 1989-1995 | Vyazynka, Konotopka, Ilija, Rybchanka | Neman |
| 6 | 43 | 1987-1993 | Drissa, Marinets, Cherneya | West. Dvina |
| 7 | 42 | 1987-1993 | Necherskaya, Studionenkaya, Svolna | West. Dvina |
| 8 | 75 | 1990-1995 | Lovat, Servaika, Uzhovsky, Skljanka, Prosimka | Lovat |
| 9 | 18 | 1990-1992 | Vymno, Rjabinka, Luzhesnjanka, Gromot | West. Dvina |
| 10 | 16 | 1993-1994 | Dubovka, Obol, Usysa | West. Dvina |
| 11 | 12 | 1993-1995 | Stracha, Golbeltsa | Neman |
| 12 | 11 | 1987-1989 | Volka, Western Berezina, Neman | Neman |
| 13 | 12 | 1991-1993 | Ptich | Pripjat |
| 14 | 22 | 1990-1994 | Svisloch | Dnepr |
| 15* | 25 | About 1960 | American mink farm in Molodechno district, Mins | k region |
| Total | 418 | | | |

^{*} founder sample

Zhivotovsky's test (Zhivotovsky 1979) was used to state the value of a phenetic distance by doing a pairwise comparison of the skull samples. This method is based on estimating both the similarity index (r) and the identity criterion (I). The similarity index, which is the measure of phenetical similarity between two samples, and might be interpreted as frequency of joint morphs (phens, variants of non-metric trait) in both of these samples, has been defined as:

$$r = \sqrt{p_1q_1} + \sqrt{p_2q_2} + \ldots + \sqrt{p_mq_m}\,,$$

where $p_1, p_2 \ldots, p_m$ are the frequencies of the m phens in the variability of the i-non-metric parameter for the first sample $(p_i < 1)$, and q_1 , q_2, \ldots, q_m are the frequencies of the same m phens in the variability of the i-non-metric parameter for the second sample $(q_i < 1)$. If the samples are compared by k non-metric parameters, then r is calculated as:

$$r = (r_1 + r_2 + ... + r_k)/k.$$

The identity criterion, as a tool for evaluation of significance of phenetic distances, has been defined as follows:

$$I = 8 n_1 n_2 (1 - r - (p_0 + q_0)/4)/n_1 + n_2,$$

where n_1 and n_2 are the sizes of the samples compared; p_0 is the sum of frequencies of phens that are presented in the first sample but not in the second one, q_0 – accordingly, is the sum of frequencies of phens that are presented in the second sample but not presented in the first one. The identity criterion I is distributed as the well

known χ -square criterion with the degrees of freedom df = m – 1. By involving k non-metric parameters for the pairwise comparison of samples, I has been defined as:

$$I = I_1 + I_2 + \ldots + I_k,$$

with the degrees of freedom calculated as $df = m_1 + m_2 + ... + m_k - k$.

Twenty-two non-metric skull parameters were used for the phenetic study of the American mink. Their variability gives 80 variants i. e. phens as typical states of the non-metric skull parameters (Figs. 2, 3). Number, presence/absence, shape and location of foramina on a particular bone and other bony structures were the basic categories of these non-metric skull variables. In case of bilateral parameters, only the right side of the cranium was taken into account.

In total, 80 phens were revealed (Fig. 3) using the following non-metric skull parameters:

- 1. Shape of the foramen infraorbitale (front view of the skull): 1.1 oval; 1.2 side bend; 1.3 bottom bend; 1.4 triangle;
- Foramen occipitale superior (back view): 2.1 one foramen directly below crista occipitalis;
 2.2 absent;
 2.3 one foramen located between crista occipitalis and foramen magnum;
 2.4 one foramen directly above crista occipitalis;
 2.5 two foramina located separately horizontally directly below crista occipitalis;
 2.6 two foramina located separately, one directly below crista occipitalis, another directly above foramen magnum;
 2.7 three and more foramina directly below crista occipitalis;

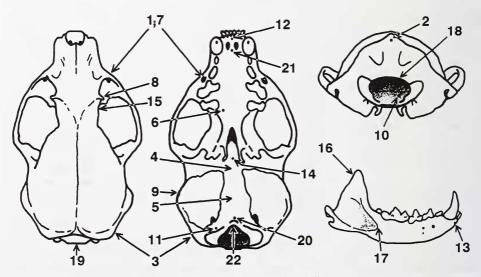


Fig. 2. Location of the non-metric parameters on an American mink skull.

| 1.1 | 1.2 | 1.3 | 1.4 | 2.1 | 2.2 | 2.3 | 2.4 | 2.5 | 2.6 |
|-----------|----------|----------|---------|----------------|----------|---------------|-------|-------|-----------------|
| fio | fio | fio | fio | ↑ • f m | ↑ | - ↑ fm | fm | fm | fm |
| 2.7 | 3.1 | 3.2 | 3.3 | 3.4 | 4.1 | 4.2 | 4.3 | 4.4 | 4.5 |
| fm | cg bt | 1 | (| 4 | ot bt | 010 | 010 | 010 | 010 |
| 5.1 | 5.2 | 5.3 | 5.4 | 6.1 | 6.2 | 6.3 | 7.1 | 7.2 | 7.3 |
| 00 | 040 | 040 | 00 | mî) | S. | | Lifio | Lifio | Lifio |
| 8.1 | 8.2 | 8.3 | 8.4 | 8.5 | 8.6 | 8.7 | 9.1 | 9.2 | 9.3 |
|) orb) | (} | (3 | \sim | 7 | £) | £) | mae | 4. | 9. |
| 9.4 | 10.1 | 10.2 | 10.3 | 10.4 | 11.1 | 11.2 | 12.1 | 12.2 | 12.3 |
| • | fm | ٨ | 3 | a | cd | | 8:3 | B & | b d |
| 12.4 | 13.1 | 13.2 | 13.3 | 13.4 | 14.1 | 14.2 | 14.3 | 15.1 | 15.2 |
| 8.28 | 貝 | 質 | 颅 |) I | Dt bt | 00 | 0,0 | £. | 3 |
| 16.1 | 16.2 | 16.3 | 16.4 | 17.1 | 17.2 | 17.3 | 18.1 | 18.2 | 18.3 |
| 1 | 1 | 2 | Λ, | Am₁ | A. | 2 | fm | fm | _ fm |
| 19.1 | 19.2 | 19.3 | 20.1 | 20.2 | 21.1 | 21.2 | 21.3 | 22.1 | 22.2 |
| * | ₹ | ₹ | bt i bt | | 18:0 | 8 8 | Bird | cd cd | رھي |

Fig. 3. Variability of non-metric parameters of American mink skulls in Belarus. fio – foramen infraorbitale, fm – foramen magnum, cd – condylus occipitalis, bt – bulla tympanicum, m¹ – first upper molar, orb – orbita, mae – meatus acusticus externus, m₁ – first lower molar.

- Profile shape of the processus jugularis ossis occipitalis (side view): 3.1 proximal bend;
 3.2 lower angle turned up;
 3.3 straight;
 3.4 upper angle turned down;
- 4. Shape of the bony micro eminencies (estimated by rubbing with an aluminium ruler) on the os sphenoidale in front of the bulla tympani (bottom view): 4.1 V-shaped; 4.2 bow-shaped; 4.3 U-shaped; 4.4 crown-shaped; 4.5 dash-shaped;
- Shape of the bony micro eminencies (estimated by rubbing with an aluminium ruler) on the os sphenoidale between the bulla tympani (bottom view): 5.1 y-shaped; 5.2 arrow backwards; 5.3 arrow forwards; 5.4 V-shaped;
- 6. Number of the foramina palatinum posterior (bottom view): 6.1 one; 6.2 two; 6.3 three and more foramina;
- Number of small foramina located above the foramen infraorbitalis (front view): 7.1 – one;
 7.2 – absent; 7.3 – two foramina;

- 8. Foramen on the processus postorbitalis ossis occipitalis (side view): 8.1 one foramen located in front of the processus; 8.2 two foramina, one in front, another at the back of the processus; 8.3 two foramina, one in front, another oblong at the back of the processus; 8.4 foramen absent; 8.5 one foramen at the back of the processus; 8.6 two foramina, both located in front of the processus; 8.7 one foramen located on top of the processus;
- 9. Foramen temporale (side view): 9.1 one foramen; 9.2 two foramina, the front one is significantly smaller; 9.3 two foramina of the same size; 9.4 foramen absent;
- 10. Foramen canalis condylaris (back view): 10.1
 one foramen; 10.2 two foramina; 10.3 one foramen with a rudiment of the horizontal partition; 10.4 one foramen with a rudiment of the vertical partition;
- 11. Presence or absence of the foramen hypoglossus (bottom view): 11.1 present; 11.2 absent;

- 12. Number of additional foramina located in front of the foramen incisivum (bottom view): 12.1 one foramen; 12.2 absent; 12.3 two foramina; 12.4 three and more small foramina;
- 13. Number of the foramina mandibulae (front view): 13.1 one foramen; 13.2 two foramina; 13.3 three and more foramina: 13.4 absent.
- 14. Foramen located on the os sphenoidale in front of the bulla tympani (bottom view): 14.1 one foramen; 14.2 absent; 14.3 two foramina;
- 15. Number of the foramina opticum (side view): 15.1 one foramen; 15.2 two foramina (partition is a little bit deeper);
- 16. Shape of the processus coronoideus mandibulae (side view): 16.1 pyramid-shaped with oval apex; 16.2 with angular hinder margin; 16.3 with acute and turned back apex; 16.4 pyramid-shaped with cut off apex;
- 17. Position of front margin of the fossa masseterica mandibulae with respect to the hinder margin of the M₁ tooth (side view): 17.1 in front; 17.2 on the same level; 17.3 behind;
- Shape of the foramen magnum (back view):
 18.1 round-shaped;
 18.2 pyramid-shaped;
 18.3 pear-shaped;

- 19. Shape of bony vault above the foramen magnum (top view): 19.1 straight; 19.2 with two eminencies; 19.3 with three eminencies;
- Presence or absence of foramen located between the condylus occipitalis (bottom view):
 20.1 present; 20.2 absent;
- 21. Position of additional foramen located behind the foramina incisivum with respect to the hinder margin of these (bottom view): 21.1 on the same level; 21.2 in front; 21.3 behind;
- 22. Shape of bend between the condylus occipitalis (bottom view): 22.1 V-shaped; 22.2 with eminencies on both sides.

Skull non-metric variability related to sex was tested using Zhivotovsky's test, and sex-dependent parameters were excluded from further analysis. Out of 22 non-metric parameters of the American mink's skull, only 5 were significantly related to sex (Tab. 2). These were not used in the analysis below. The effect of age was not tested. Distinct changes in size and proportion of mink skulls occur during the first year of life (Kruska 1979), thus only skulls belonging to adult American mink aged one year and older

Table 2. Differences between sexes (Zhivotovsky's test) according to the skull non-metric parameters of American mink in Belarus

| Non-metric parameter | n of males | n of females | r | I | df | р |
|-------------------------|------------|--------------|-------|--------|----|---------|
| 1 | 256 | 180 | 0.995 | 4.55 | 3 | > 0.200 |
| 2 | 238 | 170 | 0.984 | 12.47 | 6 | > 0.050 |
| 3 | 145 | 118 | 0.997 | 1.60 | 3 | > 0.500 |
| 4 | 162 | 93 | 0.991 | 4.26 | 4 | >0.300 |
| 5 | 144 | 89 | 0.994 | 2.46 | 3 | > 0.300 |
| 6 | 242 | 172 | 0.998 | 1.34 | 2 | >0.500 |
| 7 | 260 | 183 | 0.995 | 4.49 | 2 | >0.100 |
| 8 | 267 | 183 | 0.992 | 7.16 | 6 | > 0.300 |
| 9 | 262 | 172 | 0.996 | 3.72 | 3 | > 0.200 |
| 10 | 266 | 183 | 0.994 | 4.79 | 3 | > 0.100 |
| 11 | 263 | 182 | 1.000 | 0.00 | 1 | 0.999 |
| 12* | 260 | 176 | 0.659 | 286.64 | 3 | < 0.001 |
| 13* | 249 | 177 | 0.986 | 11.75 | 3 | < 0.010 |
| 14* | 266 | 178 | 0.992 | 7.21 | 2 | < 0.050 |
| 15 | 262 | 184 | 1.000 | 0.00 | 1 | 0.999 |
| 16* | 265 | 184 | 0.987 | 11.67 | 3 | < 0.010 |
| 17 | 265 | 184 | 0.999 | 0.94 | 1 | > 0.300 |
| 18 | 135 | 109 | 0.988 | 5.63 | 2 | > 0.050 |
| 19 | 125 | 97 | 0.996 | 1.65 | 2 | > 0.300 |
| 20 | 133 | 110 | 1.000 | 0.00 | 1 | 0.999 |
| 21 | 119 | 104 | 0.988 | 5.19 | 2 | >0.050 |
| 22* | 66 | 56 | 0.977 | 5.48 | 1 | < 0.020 |

^{*} differences between sexes are statistically significant

(1+) were used for this study. All skulls having closed sutures (Stubbe 1973 for review) were additionally tested for age using histological sections of the canine teeth (Klevesal and Kleinenberg 1969).

Results

Differences between founders and current local population fragments

Significant differences were found between the founder sample and all other samples derived from current local population fragments of naturalised American mink (Tab. 3). Especially substantial differences

Table 3. The skull non-metric differences (by complex of all non-metric parameters, df = 39) between the founder and the present local population fragments of the American mink, Belarus

| Founders compared with the sample number: | r | I | p |
|---|-------|--------|-------|
| 1 | 0.793 | 128.71 | 0.000 |
| 2 | 0.876 | 241.98 | 0.000 |
| 3 | 0.874 | 111.02 | 0.000 |
| 4 | 0.910 | 114.22 | 0.000 |
| 5 | 0.876 | 126.06 | 0.000 |
| 6 | 0.850 | 236.75 | 0.000 |
| 7 | 0.901 | 162.86 | 0.000 |
| 8 | 0.939 | 124.60 | 0.000 |
| 9 | 0.884 | 117.96 | 0.000 |
| 10 | 0.900 | 106.33 | 0.000 |
| 11 | 0.895 | 87.31 | 0.000 |
| 12 | 0.777 | 126.56 | 0.000 |
| 13 | 0.929 | 59.61 | 0.019 |
| 14 | 0.939 | 77.03 | 0.000 |

were established by comparing the founder sample with the sample 12 from Volka sampling area, Neman river catchment $(r=0.777;\ I=126.56;\ p=0.000),\ and with the sample 1 from Ushacha sampling area, Western Dvina river catchment <math>(r=0.793;\ I=128.71;\ p=0.000).$ Lower but significant phenetic differences were discovered between founders and the sample 14 from Svisloch sampling area, Dnepr river catchment $(r=0.939;\ I=77.03;\ p=0.000).$

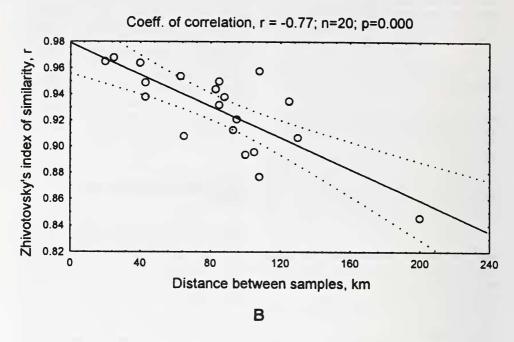
Differences among local population fragments

There were no significant differences in mean level of phenetic similarity by analysing both groups of samples (Tab. 4). Mean index of similarity was only slightly higher among local population fragments inhabiting the same river basin (0.928 vs. 0.912; p = 0.128). Also, there was no difference in rate of significantly dissimilar pairs of samples. Approximately one half of the pairwise comparisons exhibited statistically significant non-metric differences in both groups of samples (45% vs. 55%, p = 0.5). However, by comparing local samples belonging to the same basin of a large river, a significant negative correlation between the index of phenetic similarity and spatial distance between two samples was found (coefficient of correlation, r = -0.77, n = 20, p = 0.000; Fig. 4). This correlation was very low and not significant (coefficient of correlation, r = -0.24, n = 71, p = 0.842) when samples belonging to the different basins of large rivers were analysed.

Table 4. Phenetic differences between pairwise compared local samples of American mink from the same (A) and the different (B) basins of large rivers in Belarus

| Indicator | A (n = 20 pairs of samples) | B (n = 71 pairs of samples) | Significance of difference, p |
|---|--------------------------------|-----------------------------|-------------------------------|
| Rate of pairs of samples with significant difference, % | 45 | 55 | 0.500 |
| Mean r ± SD | 0.928 ± 0.0324 | 0.912 ± 0.0430 | 0.128 |
| Mean I ± SD | 64.51 ± 15.680 | 76.65 ± 33.763 | 0.123 |





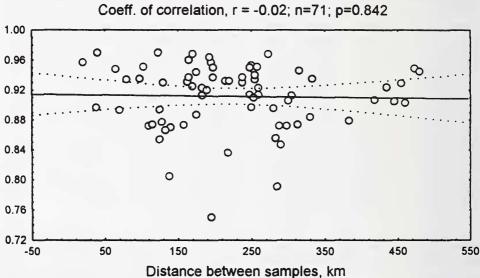


Fig. 4. Correlation between the phenetic similarity and spatial distance among local population fragments from the same (A) and different (B) large river basins (geographical populations) in Belarus.

Table 5. The non-metric skull differences (r; I; p, by complex of all non-metric parameters, df = 39) among pairwise compared geographical populations of American mink inhabiting basins of large rivers in Belarus

| Basins | W. Dvina | Neman + Dnepr | Pripjat (n = 28) |
|---|---------------------|---|---|
| Lovat (n = 79) W. Dvina (n = 222) Neman + Dnepr (n = 100) | 0.976; 150.8; 0.000 | 0.977; 102.8; 0.000 0.990; 68,8; 0.020 | 0.968; 71,2; 0.010 0.955; 118.2; 0.000 0.968; 72.3; 0.010 |

Differences among geographical populations

The non-metric differences were statistically significant, and sufficiently high to be characterised by substantial non-metric specificity between all the 4 geographical populations inhabiting the basins of the large rivers - Lovat, W. Dvina, Neman-Dnepr, and Pripjat (Tab. 5). The greatest difference was found between populations from the W. Dvina and Pripjat river basins (r = 0.955; I = 118.2; p < 0.001). These river basins are characterised by considerably different habitat conditions for American mink.

Discussion

Substantial intraspecific phenetic differentiation was found among American mink within the fairly small area of Belarus (204 000 km²). After approximately 30-40 years, established local populations were also markedly different in comparison with the founder population. This suggests a high level of adaptability of this naturalised predator to new habitat conditions. High levels of non-metric plasticity could be one of the basic factors which enabled the American mink to adapt to different ecological conditions and spread throughout Europe (Pav-LOV et al. 1974; GERELL 1967 a, b, 1968; DA-NILOV and TUMANOV 1976; DUNSTONE 1993; Sidorovich 1993, 1997).

In domesticated American mink populations, the absence of strict natural selection as well as deliberate artificial selection could lead to a certain partial "packing up" of the gene pool. In several European countries significantly lower levels of sexual dimorphism were found in domestic American mink in comparison with the feral ones (Lynch and Hayden 1995). It was interpreted as weak sexual selection, absence of competition, and purposeful artificial selection for larger specimens of both sexes. Decrease in size of brain and some other organs in the domesticated American mink may result from reductions of central nervous and circulatory functions in the domesticated organism (Kruska 1996; Kruska and Schreiber 1999).

More diverse selection started when domestic minks were placed in completely different feral conditions. The gene pool of the newly formed populations of American mink was affected by different pressures of natural selection in comparison with ranch conditions. Consequently, the phenetic structure of these populations should change. This could explain our finding that the founder population differs substantially phenetically from all the current local populations.

Non-metric skull differences among contemporary local population fragments of American mink might also be affected by stochastic changes in frequencies of variants of non-metric parameters in small spatial groups of individuals (processes of genetic drift: the bottleneck, founder effect), especially when small samples from different river catchments were compared. Spatially remote local groups of individuals belonging to different geographical populations might be phenetically similar, whereas the neighbouring ones could be phenetically very different. Absence of a correlation between non-metric and spatial distances demonstrate that phenetic relations between population fragments from the different geographical populations are rather stochastic. Such stochastic differentiation has been reported for many other species (e.g. Grewal and Dasgupta 1967; McLellan and Finnegan 1990; Kozakiewicz and Kanopka 1991; Lorenzini et al. 1993; Ryan et al. 1996).

However, presence of a significant correlation between the non-metric differences and the spatial distances among samples from the same geographical population suggests another interpretation. This finding demonstrates a certain regularity in the intrapopulational non-metric (possibly also genetic) divergence rather than the presence of a stochastic factor. Our results also demonstrate that all geographical populations of American mink (inhabiting catchments of large rivers) were phenetically specific, thus having their own "general" vector of selection. Different selective pressures within one geographical population likely result in formation of phenetically different groups of individuals. The rate of gene flow between such groups would depend on the degree of spatial isolation. Spatial distances among intraspecific groups often correlate with phenetic or genetic differences (REES 1969; McLellan and FINNEGAN 1990; ULEVIČIUS 1992). Thus, spatial isolation can influence genetic and phenetic structures.

The social intraspecific structure can lead to considerable genetic differentiation of adjacent social groups, too. It has been established in primates (Scheffrahn et al. 1996). Both genetic and environmental factors might be important for the control of phenetic variability (e.g. Petras 1967; Howe and Parsons 1967: Berry and Berry 1972: see also HARTL et al. 1993 b, for review). Some authors have argued that the genetic variation explains more than 50% of phenotypic variation (Soule and Zegers 1996). A significant part of phenetic variation can be influenced by phenotypic plasticity as a function of the environment. Genetically, plasticity is likely due to both differences in allelic expression across environments, and changes in interactions among loci (SCHEINER 1993).

Results of our study might be interpreted in connection with a very high phenetic plasticity of American mink occupying new and diverse habitat conditions. Other ecological characteristics of naturalised American mink populations in our study area confirmed the distinct ecological plasticity of this species (Sidorovich 1993, 1997). It should be emphasised that our data are not in accord with the data from some other populations of American mink. For example, American mink from Norway exhibited relatively little geographic variation in either the metrical measurements or the non-metrical traits thus indicating little genetic variation (WIIG and LIE 1979). Electrophoretical investigations on wild and ranch mink from Canada and Germany, respectively, showed low protein heterozygosity in both groups (Kruska and Schreiber 1999). These authors also reviewed works of other investigators showing low allozyme heterozygosity of mustelids. In this respect an explanation of phenetic differentiation of American mink in Belarus due to the phenetic plasticity would also be reasonable because the phenetic expression of monomorphic loci may be unequal in different environments.

For a more detailed study of mechanisms of the non-metric differentiation of American mink in Belarus biochemical-genetic investigations are needed. However, the presently discovered substantial non-metric differences in temporal and geographical scales show that an influence of genetic factor was very important.

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Zusammenfassung

Spezifität nicht-metrischer Parameter von Mink-Populationen (Mustela vison) im Verhältnis zu Habitat-Unterschieden in Weißrußland

Insgesamt 418 Schädel des Mink, Mustela vison, wurden durch eine nicht-metrische (phänetische) Studie geprüft um die Spezifität der Einzelheiten von 15 auseinander liegenden und für 4 geographische Populationen der großen Flußbecken in Weißrußland zu untersuchen. Verglichen wurden auch 14 Proben von den derzeitigen Populations-Fragmenten mit einer Probe der regionalen Gründerpopulation dieser Art. Die Distanzen zwischen den Proben wurden unter Benutzung von 22 nicht-metrischen Merkmalen abgeschätzt. Ein hohes Niveau phänetischer Divergenz wurde in den natürlichen Mink-Populationen von Weißrußland festgestellt. Die Gründertiere zeigten bedeutende phänetische Unterschiede, die mit jedem der 14 entfernten Populations-Fragmenten verglichen wurden. Beträchtliche phänetische Unterschiede werden in der Hälfte des paarweisen Vergleiches zwischen entfernten Populations-Fragmenten gezeigt. Es gab außerdem eine signifikante negative Korrelation zwischen der phänetischen Ähnlichkeit und räumlicher Entfernung unter den Populations-Fragmenten an einem einzelnen Flußbecken. Es gab keine derartige Korrelation unter Populations-Fragmenten von unterschiedlichen Flußbecken. Statistisch bedeutungsvoll waren die phänetischen Distanzen zwischen allen 4 geographischen Populationen, welche die großen Flußbecken bewohnen. Die nicht-metrische Differenzierung bei den natürlich lebenden Tieren wird unter dem Aspekt der vielfältigen Habitat-Bedingungen, in der die Population vorkommt, besprochen. Die in unserer Studie dargestellte phänetische Plastizität des Mink (welche die genetische Plastizität kennzeichnet) ist eine Anpassung, die über den hohen demographischen Erfolg dieser freilebenden Art entscheidet, was in vielen Regionen Europas und Asiens gezeigt werden kann.

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